



Permafrost landslides promote soil CO₂ emission and hinder C accumulation

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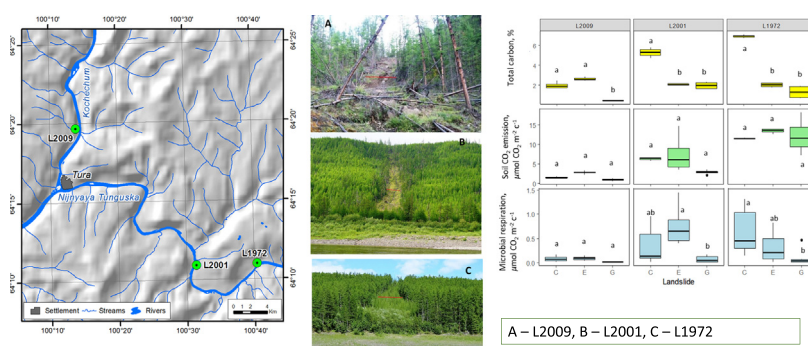
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HIGHLIGHTS

- Landslides cause high variation of soil CO₂ fluxes in permafrost areas of Siberia.
- Soil CO₂ fluxes tend to be higher at sites disturbed by landslides compared with intact larch stands.
- Landslides in the permafrost zone hinder soil carbon accumulation for long periods.
- Landslides radically transform larch communities on south-facing slopes of northern rivers.

GRAPHICAL ABSTRACT



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ABSTRACT

Landslides are common in high-latitude forest ecosystems that have developed on permafrost. The most vulnerable areas in the permafrost territories of Siberia occur on the south-facing slopes of northern rivers, where they are observed on about 20% of the total area of river slopes. Landslide disturbances will likely increase with climate change especially due to increasing summer–autumn precipitation. These processes are the most destructive natural disturbance agent and lead to the complete removal of pre-slide forest ecosystems (vegetation cover and soil). To evaluate postsliding ecosystem succession, we undertook integrated ecological research at landslides of different age classes along the Nizhnyaya Tunguska River and the Kochechum River (Tura, Krasnoyarsk region, Russia). Just after the event (at the one-year-old site), we registered a drop in soil respiration, a threefold lower microbial respiration rate, and a fourfold smaller mineral soil carbon and nitrogen stock at bare soil (melkozem) plots at the middle location of the site as compared with the non-affected control site. The recovery of disturbed areas began with the re-establishment of plant cover and the following accumulation of an organic soil layer. During the 35-year succession (L1972), the accumulated layer (O-layer) at the oldest site contained similar C- and N stocks to those found at the control sites. However, the mineral soil C- and N stocks and the microbial biomass – even of the oldest landslide area – did not reach the value of these parameters in control plots. Later, the soil respiration level and the eco-physiological status of soil microbiota also recovered due to these changes. This study

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demonstrates that the recovery after landslides in permafrost forests takes several decades. In addition, the degradation of permafrost due to landslides clearly hinders the accumulation of soil organic matter in the mineral soil.

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1. Introduction

In recent decades, many questions have arisen concerning the threat of permafrost degradation under changes in northern latitudes. Most researchers point to the direct connection between current global climate change and substantial permafrost degradation (IPCC, 2013; Jorgenson and Grosse, 2016). Romanovsky et al. (2010) have reported that permafrost temperatures have increased by up to 2 °C in Siberian regions over the last 40 years, whereas the air temperature increased 1–3 °C from 1960 to 2010 (Tchebakova et al., 2011). According to Shan et al. (2015), the average annual temperature in the permafrost area of China has increased by 3.2 °C over the past 60 years. A warming trend in atmospheric temperature in Iceland has been observed over the last two centuries – an increase of about 0.7 °C per century (Nawri and Björnsson, 2010). Some important negative consequences of permafrost degradation for the environment likely include intensive emissions of greenhouse gases (GHG) stored in permafrost soil organic matter in high-latitude regions in Siberia (Russian Federation) (Wagner et al., 2007; Wagner et al., 2009; Gentsch et al., 2015) and dissolved organic carbon that is laterally transferred to aquatic ecosystems (Osudar et al., 2016; Liu et al., 2018). GHG released from thawing permafrost is the greatest form of terrestrial feedback and – in turn – amplifies atmosphere warming and further permafrost degradation (Abbott and Jones, 2015). Although some recent studies have been undertaken on dark soil CO₂ fixation, which can be accounted for as a re-use of 0.1–5% of net soil respiration value in permafrost soils (Šantrůčková et al., 2018), this dark soil CO₂ fixation is likely unable to compensate for GHG emissions in high latitudes due to climate change.

In boreal ecosystems, wildfires are considered to exert the greatest influence on permafrost degradation (Flannigan et al., 1998; Wondzell and King, 2003; Kharuk et al., 2011), followed by pathogen and insect outbreaks (Eng et al., 2004) and timber harvesting (Smith et al., 1986). Ground forest fires often occur in the permafrost region of Siberia. This type of wildfire burns vegetation cover and litter, but the tree layer can survive, and the mineral soil remains undisturbed (Masyagina et al., 2015). At the beginning of 21st century, another disturbance agent rose to prominence in permafrost degradation: landslide processes (e.g. solifluctions), which have increased in the permafrost zone of central Siberia (Abaimov et al., 2002; Geertsema and Schwab, 2004; Kharuk et al., 2016) and generally occur on south-facing river slopes (Prokushkin et al., 2010). In this region of Siberia, landslides cause more disturbances to forest ecosystems and permafrost than do wildfires or timber harvesting since solifluction eliminates entire ecosystems, including vegetation and productive soil (Shishov et al., 1999; Prokushkin et al., 2010), thereby resulting in C- and N loss in addition to a radical alteration of wildlife habitat. Prokushkin et al. (2010) assessed the loss of C from the mineral soil (18000–88000 kg C ha⁻¹), live wood (13000–24000 kg C ha⁻¹), and O-horizon (8000–12000 kg C ha⁻¹) in the same landslides as in our study (L2001 and L1972). Carbon loss with mineral soil due to landslides in Tura is comparable to or greater than carbon loss from thermokarst (12 kg C m⁻²; Abbott and Jones, 2015). Soil landslides usually occur in the thickest soil active layer (e.g. south and west slopes) and can be triggered by biotic (pathogen- and insect outbreaks) and abiotic disturbance agents (wildfires, logging) or local climate anomalies, such as the overwetting of seasonally thawed layers due to climate change (due to a combination of high air- and soil temperatures and excessive precipitation in summer, or intensive snow thawing) (Kharuk et al., 2016).

During landslides, the removal of top soil means that new ecosystem succession begins atop parent material. In the first years after a

landslide, local temporal streams form due to the melting of the outcropping permafrost layer. At the same time, erosion begins after landslides, and a large amount of soil and organic material enters streams as sediment, which results in the deterioration of water quality (Geertsema et al., 2009). Moreover, the washout of humus and nutrients from soil accumulative horizons alters soil fertility properties (Sorokin et al., 2005; Prokushkin et al., 2010). New ecological conditions occur at areas disturbed by landslides and result in changes to the environment, species composition, soil carbon- and nitrogen stocks, soil respiration fluctuations, soil microbial community variation, and soil GHG emissions (Prokushkin et al., 2010; Masyagina et al., 2013). These factors, in turn, initialize the first phase of recovery (succession) for the newly forming ecosystem. Landslides are an important factor in landscape-formation and help to increase site and habitat diversity (Pozdnyakov, 1986; Abaimov et al., 2002; Geertsema and Pojar, 2007). Various heterogeneous conditions (microclimatic and edaphic) develop at the location of a landslide, especially on permafrost soils. Landslide areas of various ages and types therefore represent a mosaic of successional stages across landscapes. Landslides impact soil chemistry: the availability of C, N, and P along with the base cations (Ca, Mg, K) and pH values are different in soils subjected to landslides compared with intact soil, and the C/N ratio is affected by landslides (Pozdnyakov, 1986; Huggett, 1998). Thus, soil C- and N stocks, soil microbial activity, vegetation regeneration, and soil respiration are highly variable at different microsites (e.g. depending on microtopography). However, the thermokarst disturbance type of landslides also delivers organic matter to downslope or downstream ecosystems (sometimes as rafted intact blocks), where it may or may not be released to the atmosphere (Abbott and Jones, 2015). Wildfires, on the other hand, promote to send the directly mineralized organic matter to the atmosphere. During a landslide, an active layer of soil (together with vegetation) slides down on a ruptured permafrost surface and can accumulate downslope, thereby enabling the preservation or stabilization of soil carbon over a long period. In recent decades, the formation and consequences of landslides – as well as soil-vegetation regeneration patterns – in high latitudes have attracted little attention, though an increase in the number of landslides in permafrost areas is of great concern to global change (Prokushkin et al., 2010; Kharuk et al., 2016). For example, in 2001, 72 solifluction areas were observed within 100 km of the middle stream of Nizhnyaya Tunguska River (Siberia) (Abaimov et al., 2002). From 2000 to 2012, Kharuk et al. (2016) found 145 landslides in a 62000-km² territory located just the north of Tura via an analysis of satellite imagery. In Alaska, landslides in permafrost terrain have also increased in size and mobility (Coe et al., 2018).

In the present study, we address the changes in physical, chemical, and biological parameters along landslide chronosequences. Our main hypothesis is that permafrost landslides (via the example of larch ecosystems in the permafrost region of Siberia) promote soil CO₂ emission due to the acceleration of soil microbial processes in more favourable microenvironments (increased soil temperature and sufficient water content) and in the abundant substrate exposed after a landslide disturbance. We additionally examine whether landslides cause transformation in the soil microbial community and biotope structure or bring changes in biological species diversity.

2. Study area and site characteristics

The study area is located in the northern part of central Siberia (Tura, Krasnoyarsk region, Russian Federation) in an area underlain by

continuous permafrost. This region has a cold continental climate and a mean annual temperature of -9.5°C with a mean monthly temperature ranging from -36°C in January to 16°C in July. The region's average annual precipitation is 300–350 mm, about 30–40% of which falls as snow, which averages 40–50 cm per year. The growing season is about 115 days, with a frostless period of 55–56 days (Butorina, 1979).

In order to study the effects of different solifluction stages on forest successions based on age class and degradation level, we selected three sites disturbed by landslides of different age classes on southeast- and southwest-facing slopes in a valleys of the Nizhnyaya Tunguska River and the Kochechum River (64°N 100°E , Figs. 1–2, Tables 1–2). Along with landslide sites, adjacent control plots (intact and undisturbed by the landslide) were chosen to estimate the effect of soil sliding on ecosystem processes. The control sites are described as larch stands (*Larix gmelinii*, Rupr. Rupr.). The total area affected by landslides (zone of depletion and accumulation) was about 1165 m^2 for L2009, 11200 m^2 for L2001, and 5700 m^2 for L1972 (Table 1). The chosen areas are characterized by different types of forest, amounts of mineral- and organic matter, and ecological conditions. Moreover, a successful regeneration of Gmelin larch (*Larix gmelinii*) has been observed at all solifluction sites (Prokushkin et al., 2010).

Our surveys were conducted in the midslope positions at the three landslide sites every August from 2004 to 2013 (Tables 1–2, Figs. 1–2). We surveyed $3 \times 3\text{-m}$ plots along 20-m transects at every landslide site as well as at a control-adjacent stand in the middle part of the slope. These small plots were used for soil sampling, field measurements of soil respiration and temperature, plant species composition description, and the estimation of cover values. In order to study the variability of environmental conditions and microtopography caused by landslide disturbance, we established two types of small plots ($3 \times 3\text{ m}$) at landslide sites: the Edge microsite (E-plots) and the Ground microsite (G-plots). The E-sites represent the boundary layer between the intact stand and the one destroyed by solifluction. In the edge plots, there was a mixture of soil and woody debris that has allowed for the survival of some forest species. Between the edges, there were established G-plots that represent a fine-grained layer (bare ground, melkozem), with no plants persisting after the landslide event. In total, we established 27 small plots ($3 \times 3\text{ m}$) in landslide and control sites. Due to landslide effects, the edges and central zones (bare ground) have drastically changed with respect to nutrient contents and ecological conditions (Prokushkin et al., 2010).

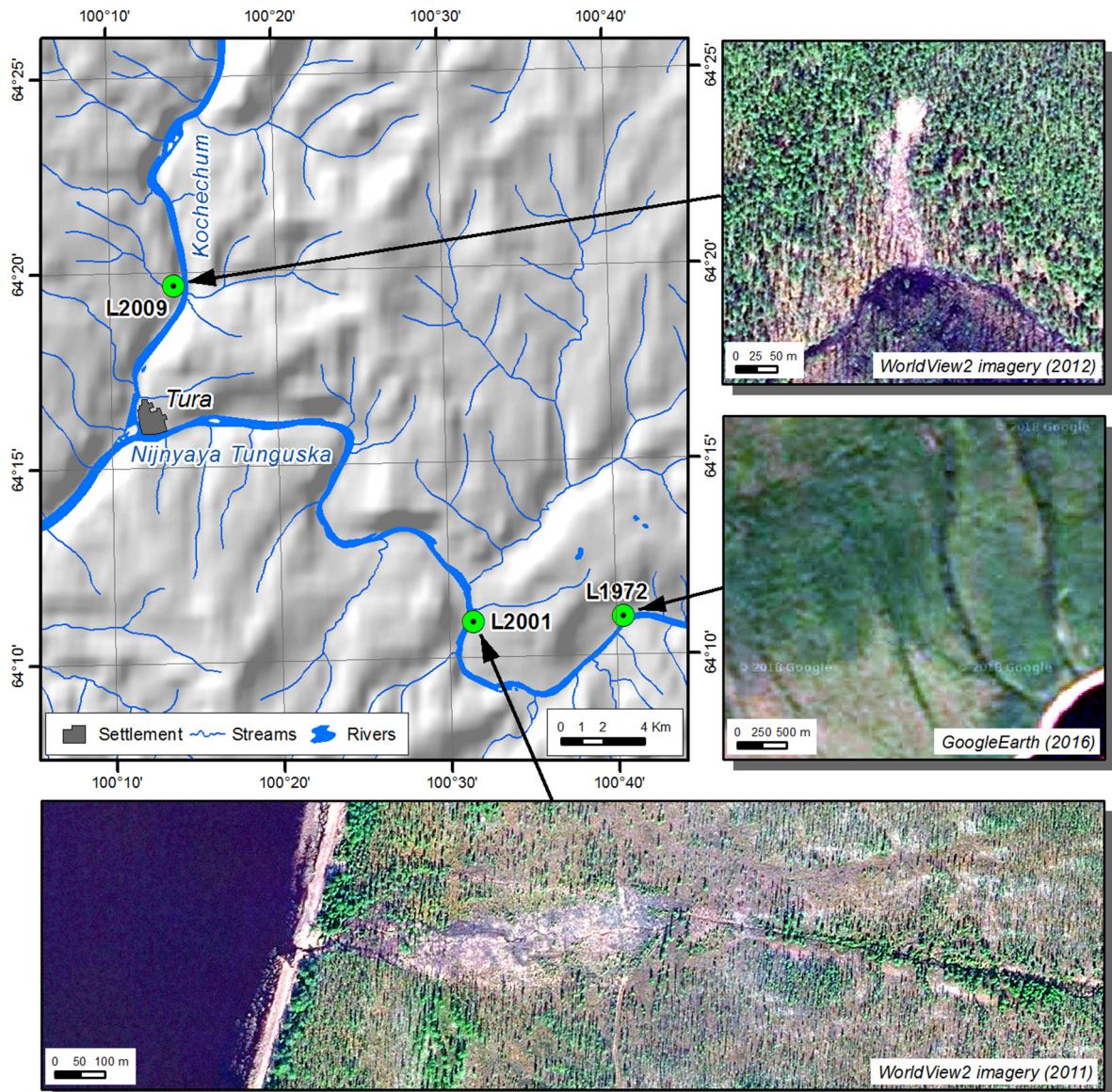


Fig. 1. Location of study sites and satellite views of studied landslides (L2009–3 years old as of 2012; L2001–10 years old as of 2011; L1972–44 years old as of 2016).



Fig. 2. Landslides studied after (A) one year (L2009 as of 2010), (B) six years (L2001 as of 2007), and (C) 35 years (L1972 as of 2007). Red line points to the middle part of landslide area (photo by Masyagina O.V.).

3. Methods

3.1. Field measurements

The quantity of vascular plants, moss, lichen species (pcs), and *Larix* seedlings (pcs ha⁻¹) was measured within small plots (3 × 3 m) located in the middle part of the slope along the red line shown in Fig. 2 before soil respiration- and temperature measurements were taken. Descriptions of the composition of plant species at the control- (intact) and landslide communities were made according to standard geobotanical methods (Sukachev and Zonn, 1961; Ponyatovskaya, 1964; Westhoff and Maarel, 1973; Andreeva et al., 2002) in 2004 (for L2001, L1972, and adjacent control sites) and in 2013 (for L2009 and its control site). The names of the vascular plant species were determined according to Cherepanov (1995), and the names of lichens and bryophytes

were determined according to Konstantinov et al. (1992), Andreev et al. (1996), Ignatov et al. (2006), and “A Checklist of the Lichen Flora of Russia” (2010).

Soil respiration rates (SR, $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) were measured at small plots (3 × 3 m) on the base of 3–5 soil polyvinylchloride (PVC) collars (D = 10 cm) with Li-Cor 6200 (LI-COR, USA) at landslide- and control sites in July of 2007 and 2009.

Soil temperature (ST, °C) was measured at a depth of 5 cm with an electronic thermometer Checktemp 1 (USA) at the same time that the soil respiration was measured. A 5-cm depth was chosen because it is an important depth for the root systems of juvenile plants. Furthermore, we decided to measure the ST instead of measuring the litter layer because the litter layer is usually removed by solifluction at landslide plots.

3.2. Field sampling

To assess how soil sliding at each site affected ecosystem recovery in August 2007 (for L2001 and L1972) and in August 2009 (for L2009), mineral soil samples were collected at each site in August for C-, N-, and mineral soil water content analyses as well as for incubation experiments that measured soil heterotrophic respiration (MR) and soil microbial biomass (MB). Soil samples for soil microbial community structure and PCR analyses were obtained at the control site, and E-plots and G-plots at L2001 and L1972 in August 2010. Mineral soil samples were excavated down to the top 5 cm of soil in the active layer with 3–4 repetitions and were kept in the refrigerator at 4 °C until aircraft transportation. After the flight, the samples were transported to the laboratory and processed.

3.3. Laboratory analyses and incubation

Gravimetric mineral soil water content (MSWC, %) was determined in soil samples collected at a depth of 0–5 cm at the same time that soil respiration was measured.

To study mineral soil C, N stocks, and the C/N ratio, mineral soil samples from a depth of 5 cm were sieved to obtain <2 mm fraction, and the

Table 1
Landslide sites characteristic.

Parameter	L2009	L2001	L1972
Year of the landslide event	2009	2001	1972
River valley	Kochechum	Nizhnyaya Tunguska	Nizhnyaya Tunguska
Direction	Southwest	Southeast	Southwest
Location	64.328 N 100.231E	64.182 N 100.525E	64.183 N 100.675E
Time elapsed since disturbance (years)	1 (as of 2010)	6 (as of 2007)	35 (as of 2007)
Slope inclination, dip (steepness) (°)	15–25	19–27	11–20
Slope length (m)	95	390	290
Maximum width of site (m)	15	33	37
Minimum width of site (m)	14	12	7
Site area (m ²)	1165	11,200	5700
Volume of washout of soil (m ³)	252	5365	3725
Loss of wood (m ³)	ND	72.8	91.2
Height of vegetation cover and litter (L2001 and L1972 as of 2007, L2009 as of 2013), (cm)	0.1	1.1 ± 0.6	5.7 ± 0.9

ND – no data.

Table 2
Control site characteristics.

	C2009	C2001	C1972
Stand type adjacent to middle part of landslide	<i>Vaccinium</i> dry moss larch stand (dominated by <i>Rhytidium rugosum</i> (Hedw.) Kindb.)	<i>Ledum-Vaccinium</i> green moss larch stand (dominated by <i>Pleurozium schreberi</i> (Brid.) Mitt.)	<i>Ledum-Vaccinium</i> green moss larch stand (dominated by <i>Pleurozium schreberi</i> (Brid.) Mitt.)
Soil type ^a	Typic Aquorthels	Typic Aquorthels	Typic Aquorthels
Tree species composition	7L3P	10 L	10 L
Age, years	100–200	150	90–150
Mean H, m	12	13	9
Mean D, cm	20	14	10
Crown closure	0.6	0.4	0.7
Forest yield, m ³ ha ⁻¹	110	50	90

^a *Keys to soil taxonomy* (1998). Note: L – *Larix*, P – *Picea*.

contents were then determined on a Vario Isotope Cube analyser coupled with IRMS (Elementar, UK/Germany) after the soil samples had been dried at 60 °C for 48 h.

Soil heterotrophic microbial biomass (MB, mg C g⁻¹ of dry soil) was assessed via substrate-induced respiration (SIR, mg C g⁻¹ of dry soil hour⁻¹) determination with subsequent recalculation of microbial biomass carbon (C-CO₂) according to Eq. (1) (Sparling, 1995). To assess SIR values, fresh mineral soil (2 g) of soil water capacity equal to 60% was placed in 15-ml glass flasks, to which 0.1 ml of a glucose-mineral solution was added to achieve a glucose concentration equal to 10 mg g⁻¹ of soil. Afterwards, flasks were closed hermetically with resin stoppers and incubated at 22 °C. Soil gases from flasks were taken twice: first, just after the glucose-mineral mixture was added, and second, after a few hours. The CO₂ concentration was analysed with the gas chromatographer Agilent 6890N at a Collective Using Center of Sukachev Institute of Forest SB RAS (Krasnoyarsk, Russia) (Masyagina et al., 2015).

$$MB = 50.4 \times SIR \quad (1)$$

A microbial respiration (MR, μmol CO₂ m⁻² s⁻¹) of soil microbiota as a CO₂ emission rate was obtained during 24 h of soil incubation at 22 °C and 60% of soil water capacity (Masyagina et al., 2015).

A coefficient of microbial activity qCO₂ (Sparling, 1995; Ananieva, 2003) was calculated with Eq. (2).

$$qCO_2 = MR/MB \quad (2)$$

DNA extraction for quantitative PCR was performed using the Power Soil™ DNA Isolation Kit (Mo Bio laboratories Inc., Carlsbad, California, USA) according to the manufacturer's protocol. DNA templates for qPCR analyses were extracted from three biological replicates. Quantitative PCR was performed on a CFX96 thermocycler (Bio-Rad Laboratories, Inc., Hercules, USA). Each reaction contained an iQ Mastermix (10 μl; Bio-Rad Laboratories, Inc., Hercules, USA), PCR primers (1 μl containing 10 pmoles μl⁻¹ each), sterile water (6 μl), SYBR® Green (0.2 μl per reaction of 100 × diluted from 10000 × concentrate), and a DNA template (5 μl), which were all added to a final volume of 20 μl. Primers targeting bacteria were used (EUB331-F/EUB797-R). The qPCR reactions comprised an initial denaturation (10 min at 95 °C), followed by 39 cycles of 30 s at 95 °C, 30 s at 57 °C, and 40 s at 72 °C. The qPCR assays were calibrated using known amounts of PCR amplified and cloned 16S rRNA gene fragments from corresponding taxa. The cycling program included a melting curve from 60 to 95 °C, with 0.5 °C steps per plate read. Data were analysed using the CFX Manager™ Software (Bio-Rad Laboratories Inc., USA). The quality of the qPCR results was checked using gel-electrophoresis, and the results of gel electropherography after qPCR (Bacteria) (qPCR 16 s general Bacteria, primer combination: Eub331-F/Eub797-R) revealed the signature of the functional type of microbe.

To assess the abundance of soil microbial communities, we used a method of surface plating on Petri dishes that contained dense nutrient medium. After growth on agar plates, the abundance was calculated by

colony counting (*Methods of soil microbiology and biochemistry*, 1991). 20–30 ml of medium containing agar-agar was put in Petri dishes, and after hardening at room temperature, all Petri dishes were turned over to prevent condensation of water on the agar surface. After preliminary soil solution dispersion, a 1:1000 dilution of soil suspension solution was made. This diluted solution was plated on Petri dishes in three repetitions. The plated dishes were turned over and placed into a thermostat device at 28 °C. Bacteria colonies were calculated after 3 days, actinomycetes colonies after 7–20 days, and fungi and yeast colonies after 5–7 days. After the colonies on Petri dishes had been calculated, we determined the mean number of colonies per 1 g of dry soil according to the Eq. (3) (*Methods of soil microbiology and biochemistry*, 1991):

$$a = b * c * d / e, \quad (3)$$

in which *a* represents the cell number in 1 g of dry soil, *b* the mean number of colonies in Petri dishes, *c* the dilution of the soil suspension solution, *d* the number of drops in a 1 ml suspension, and *e* the weight of dry soil taken for analysis.

We used the following nutrient mediums for quality and quantity characteristic of soil microflora:

A starch-and-ammonia medium was used for actinomycetes and bacteria determination (g per litre of tap water) that consisted of (NH₄)₂SO₄ (2 g), K₂HPO₄ (1 g), MgSO₄ (1 g), NaCl (1 g), CaCO₃ (3 g), soluble starch (10 g), and agar-agar (20 g). The starch was first mixed with a small amount of water and then added to the medium.

The meat infusion agar medium for bacteria accounts consisted of meat broth, peptone (10 g l⁻¹), NaCl (5 g l⁻¹), and agar-agar (20 g l⁻¹), and the solution was raised to pH 7.

Lockheed's soil agar medium consisted of K₂HPO₄ (0.2 g), agar-agar (20 g), and soil extract (1 l). The soil extract was prepared from strongly ameliorated fertilized soil. Sifted soil (3 mm mesh) was mixed with an equal amount (by weight) of tap water. The mixture was autoclaved for 1 h at 120 °C, and the hot suspension was then filtered through a paper filter via pumping.

Wort agar medium was prepared from a diluted wort solution with a sugar content of about 4–5°B. Agar-agar (20 g l⁻¹) was added to the mixture, and the solution was raised to pH 7. Before plating, streptomycin was added to the suspension to prevent bacteria growth.

The total value of microorganisms was calculated as a sum of all colonies (thousands of colony-forming units (CFU), g⁻¹ of dry soil) observed at all applied mediums: starch-and-ammonia medium, meat infusion agar medium, Lockheed's soil agar medium, and wort agar medium. Hydrolytic microflora were grown on meat infusion agar medium, copiotrophs on starch-and-ammonia medium, oligotrophs on Lockheed's soil agar medium, and microscopic fungi on wort agar medium (Dobrovolskaya et al., 1990).

3.4. Data analyses

The studied parameters (ST, MSWC, C, and N availability, C/N, SR, MR, MB, qCO₂, DNA amount, the number of soil microbiota groups, and plant

species) were tested for normality prior to analysis to stabilize variance, and the non-normally distributed variables were logarithmically transformed. A two-way factorial analysis of variances (ANOVAs) was used to test the main effects of the age class of the landslide and microsite types (E- and G-plots) on the variables of ST, MSWC, C, and N availability, C/N, SR, MR, MB, qCO₂, PCR, the number of soil microbiota groups, and plant species (Table 3). Tukey HSD (p adjusted) was used for Tukey multiple comparisons of means. The analyses of the obtained data were performed using RStudio version 1.1.423 – © 2009–2018 RStudio, Inc.

4. Results and discussion

The landslide is an important geomorphic agent that affects mesorelief and microrelief formation along northern Siberian rivers (Pozdnyakov, 1986). Periodic landslides at southeast- and southwest-facing slopes form gullies and ridges and influence plant communities on slopes. Climate change is expected to increase the impact of landslides in high-latitude ecosystems. This paper thus studied both long- and short-term changes in important parameters of ecosystems after landslide disturbance in high-latitude forest communities, including how forest recovery develops.

4.1. Landslide disturbance influence on the microenvironment

Hydrothermal conditions play a crucial role during the primary stage of landslide ecosystem succession (Masyagina et al., 2013). In our survey, both soil temperature at a depth of 5 cm and mineral soil water content at a 0–5-cm soil horizon were important factors in landslide plots (Table 3). Temperature-regime (at a depth of 5 cm) measurements revealed increased mineral soil temperature values at landslide sites compared with control sites. We observed a significant difference in ST values between landslide plots and intact communities, especially in the first post-landslide years (1–7 years) (Fig. 3). At L2009 (the site of

the initial successional stage), one year after a landslide event, ST was 10 °C higher at E-plots and 17.6 °C higher at G-plots compared with the adjacent intact stand. At the L2001 site, 4–7 years after disturbance, ST values were 12 °C higher at E-plots and 15 °C higher at G-plots compared with the adjacent control stand. These significant observed differences were caused by the lack of tree cover (Prokushkin et al., 2010), especially at the central part, which contained bare soil (G-plots). Abbott and Jones (2015) also assessed soil temperature as a main environmental factor in arctic thermokarst as an important predictor of ecosystem respiration. Even after 33–35 years (L1972), there was still statistical evidence of a 2 °C difference in ST between control plots and G-plots, which may point to the achievement of the final successional stage. Therefore, restoration of soil temperature to the intact community's level was provided by the re-establishment of ground moss-lichen cover and its thermal insulating properties.

Soil water content is another important ecological factor related to the recovery process of the disturbed ecosystem. Mineral soil water content at a 0–5 cm horizon did not vary greatly among intact larch stands and was in the range of 14–46%. In the first year after a landslide (L2009), there were statistically lower values of MSWC at G-plots compared with the intact stand. At L2001, 5–6 years after the disturbance, the same difference between median values of MSWC between G-plots and control plots was observed; however, this difference was not statistically significant (Fig. 3). 35 years after the landslide disturbance (L1972), the difference between MSWC values was minimal at both damaged and control sites.

The specific role of microtopography conditions in a permafrost area requires emphasis. The consequences of landslides – as well as wildfires and clear-cutting – are complicated in cryogenic soils. For example, the range and degree of the environmental transformation of ecosystems that are disturbed by landslides vary widely and can give rise to a variety of different communities. A highly varied microenvironment that has developed due to landslide disturbance provides favourable conditions (high ST and sufficient MSWC) for successful seed germination and the further prevalence of vascular plant species. Increased insolation due to the absence of shading from trees and shrub layers also contributes to these favourable conditions. Due to the high variability of hydrothermal conditions, the time of succession and environment transformation is also non-homogenous. Finally, the development of ground cover plants and tree seedlings leads to the stabilization of soil temperature, the restoration of the thermal insulating moss and lichen cover (Porada et al., 2016), and the upward growth of the permafrost table.

4.2. Landslide disturbance influence on C- and N availability

The carbon- and nitrogen stocks in the mineral soil at all landslide sites were significantly smaller (2–6 times) than those of the control sites (Fig. 4). This finding was supported by Prokushkin et al.'s (2010) studies at the same sites (L2001 and L1972); additionally, the authors observed the decreasing of pH and availability of biogenic elements (C, N, P, K, Ca), particularly at G-plots. According to Leibman (2009), these changes can be attributed to geochemical processes on slopes exposed by landslides, which can cause a redistribution of elements within the active layer and the upper permafrost. Moreover, in the middle part of the landslide, the topsoil (enriched in organic matter) was lost via landslide disturbance at our sites (bare ground). C/N values in mineral soil (0–5 cm) at landslide sites varied more widely (from 17 to 24) than did those of the control sites (from 20 to 24). All these factors can influence the structure of soil microbial biotope communities and consequently also successional processes.

4.3. Landslide disturbance influence on soil CO₂ emission and microbial activity

Soil respiration measurements conducted in the natural environment revealed slightly higher values at E-plots for all solifluction sites

Table 3

Statistical results (F-values) of two-way ANOVAs for some physical, chemical, and biological parameters at landslides in the permafrost zone.

Source of variation	Landslide	Microsite	Landslide: Microsite
Soil temperature at 5 cm depth, °C	124.1**	582.8**	178.2**
Mineral soil water content at 0–5 cm horizon, %	20.51**	5.57**	1.04
Total soil C at 0–5 cm horizon, %	55.35**	236.90**	63.51**
Soil organic C at 0–5 cm horizon, %	0.56	10.79**	1.44
Total soil N at 0–5 cm horizon, %	66.37**	161.36**	44.56**
C/N at 0–5 cm soil horizon	27.46**	26.22**	6.39**
Soil respiration, $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$	47.05**	4.77**	0.83
Microbial respiration at 0–5 cm mineral soil horizon, $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$	15.56**	11.81**	6.12**
Microbial biomass at 0–5 cm mineral soil horizon, mg C g ⁻¹ dry soil	3.11*	8.81**	1.97
qCO ₂	38.36**	9.55**	2.90**
A number of 16S rRNA genes, mln. fragment copies g ⁻¹ soil	8.75**	7.97**	0.74
A number of hydrolytic microflora colonies, thousands of CFU g ⁻¹ dry soil	4.95**	13.27**	8.20**
A number of microscopic fungi colonies, thousands of CFU g ⁻¹ dry soil	2.96	1.09	1.49
A number of copiotrophs colonies, thousands of CFU g ⁻¹ dry soil	21.64**	7.63**	10.34**
A number of oligotrophs colonies, thousands of CFU g ⁻¹ dry soil	21.98**	14.64**	24.56**
A number of actinomycetes colonies, thousands of CFU g ⁻¹ dry soil	0.20	3.60**	15.79**
A number of vascular plant species, pcs.	3.55*	10.64**	2.84*
A number of moss species, pcs.	8.30**	9.57**	2.28
A number of lichen species, pcs.	13.94**	17.43**	3.10*
Total species number, pcs.	0.76	1.68	1.10
Larix seedlings, thousands of pcs. ha ⁻¹	511.8**	1111.1**	215.8**

* P < 0.05.

** P < 0.01.

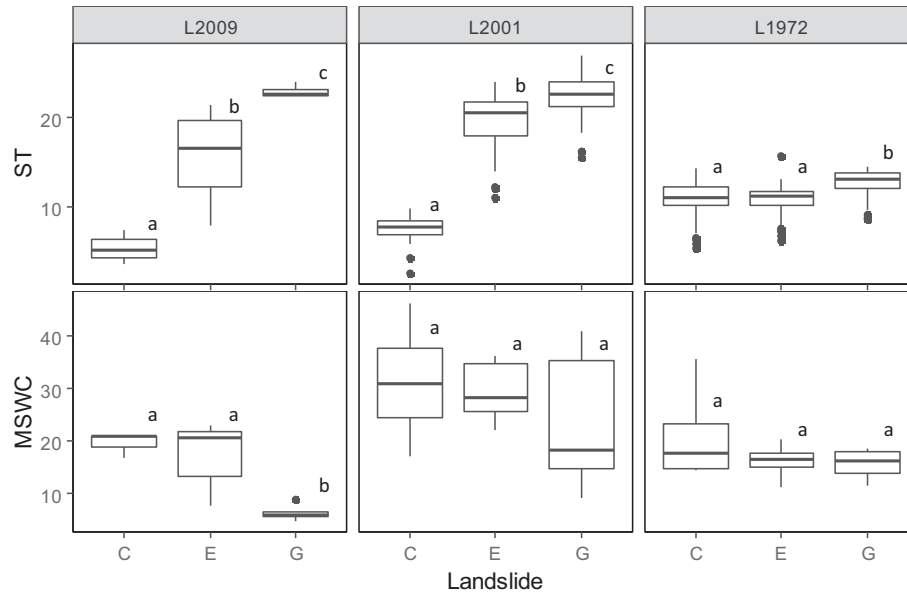


Fig. 3. The effect of landslides and their microsite type (E – right and left edge of landslide; G – ground; C – control) on soil temperature at a depth of 5 cm (ST, °C) and mineral soil water content (MSWC, %) at a depth of 0–5 cm in mineral soil horizon at landslides of different ages (L2009, L2001, L1972). The values are arranged as boxplots (medians with confidence intervals, min, max). The horizontal line within the box indicates the median, the box boundaries indicate the 25th- and 75th percentiles, the whiskers indicate the highest and lowest values, and the dots above or below the whiskers indicate the outliers. Medians followed by different letters in the same curve are significantly different at $P < 0.05$ according to Tukey multiple comparisons of means analyses.

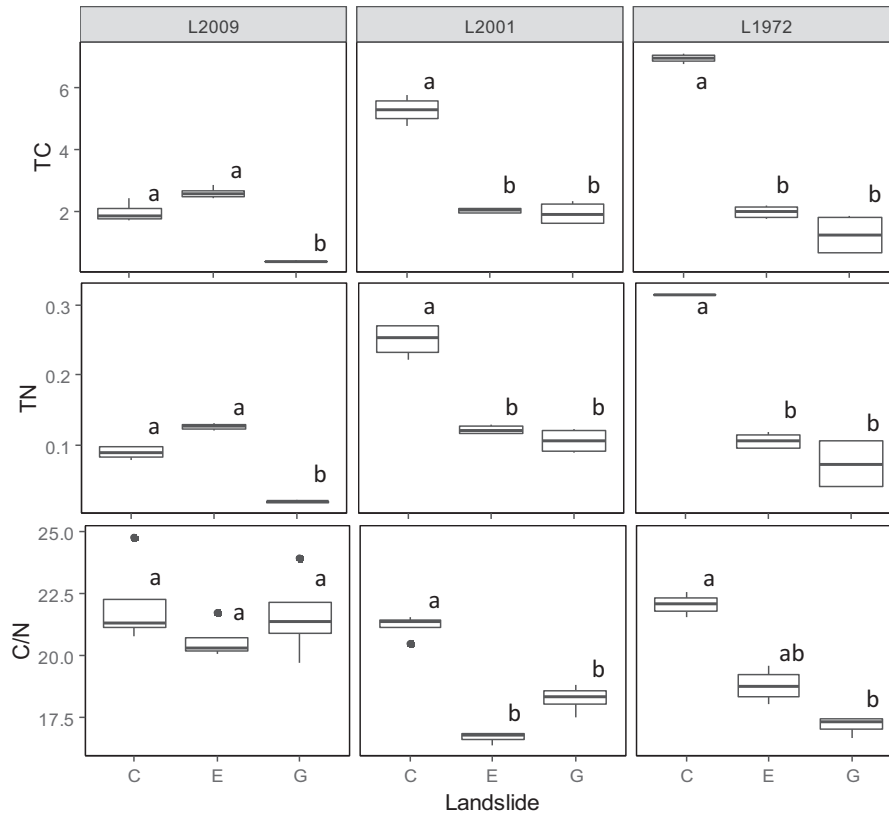


Fig. 4. The effect of a landslide and its microsite type (E – right and left edge of landslide; G – ground; C – control) on the total carbon stock (TC, %), total nitrogen stock (TN, %), and C/N values at 0–5 cm mineral soil horizon at landslides of different ages (L2009, L2001, L1972). The values are arranged as boxplots (medians with confidence intervals, min, max). The horizontal line within the box indicates the median, the box boundaries indicate the 25th- and 75th percentiles, the whiskers indicate the highest and lowest values, and the dots above or below the whiskers indicate the outliers. Medians followed by different letters in the same curve are significantly different at $P < 0.05$ according to Tukey multiple comparisons of means analyses.

compared with adjacent control communities. Due to the high variation of soil respiration values ($1.25\text{--}11.8\ \mu\text{mol CO}_2\ \text{m}^{-2}\ \text{s}^{-1}$ at control sites, $0.37\text{--}14.8\ \mu\text{mol CO}_2\ \text{m}^{-2}\ \text{s}^{-1}$ at E-plots, and $0.53\text{--}18.2\ \mu\text{mol CO}_2\ \text{m}^{-2}\ \text{s}^{-1}$ at G-plots) caused by site microtopography, these differences were not statistically significant (Fig. 5). At L1972, we also observed a high variability in soil respiration at G-plots, which can be explained by the development of microtopographic elements at G-plot environments during reforestation and successional processes (ecological competition, niche formation, etc.). In comparing landslides of different age classes and successional stages, we found that soil respiration at young landslide sites (L2009 and L2001) was not statistically different, but soil CO_2 emission at old solifluction site (L1972) was twice ($P <$

0.0001) as high as that at younger site. Soil respiration at all studied intact stands varied: it increased ($P < 0.0015$) in a range of landslides (L2009–L2001–L1972), thereby demonstrating a wide variety of microtopography conditions among the studied sites. In boreal ecosystems, microtopography is determined by cryoturbation processes and can be a source of high variability not only in environmental factors (ST, MSWC) but also in biological parameters (e.g. soil microbial activity).

Microbial respiration varied widely both at intact stands and at sites disturbed by landslides, as did the total soil respiration (for the same reasons) (Fig. 5). At the site of a one-year-old landslide (L2009) and its adjacent intact stand, soil microbial respiration tended to be higher

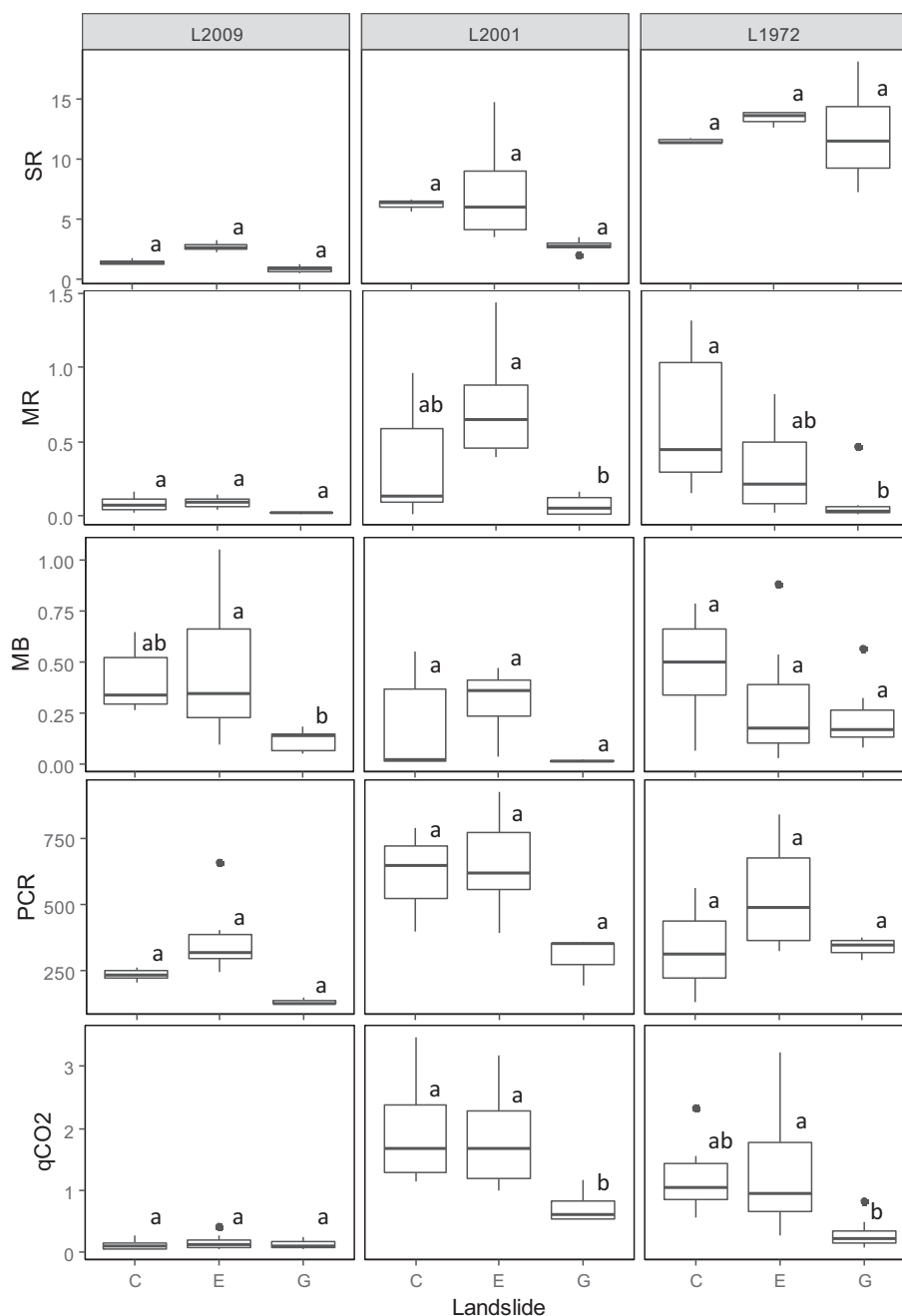


Fig. 5. The effect of a landslide and its microsite type (C – control plot; E – right and left edge of landslide; G – ground; C – control) on soil respiration (SR, $\mu\text{mol CO}_2\ \text{m}^{-2}\ \text{s}^{-1}$), microbial respiration at 0–5 cm mineral soil horizon (MR, $\mu\text{mol CO}_2\ \text{m}^{-2}\ \text{s}^{-1}$), microbial biomass at 0–5 cm mineral soil horizon (MB, mg C g⁻¹ dry soil), the amount of 16S rRNA genes (mln. fragment copies per g of dry soil), and qCO₂ values at 0–5 cm mineral soil horizon at landslides of different ages (L2009, L2001, L1972). The values are arranged as boxplots (medians with confidence intervals, min, max). The horizontal line within the box indicates the median, the box boundaries indicate the 25th- and 75th percentiles, the whiskers indicate the highest and lowest values, and the dots above or below the whiskers indicate the outliers. Medians followed by different letters in the same curve are significantly different at $P < 0.05$ according to Tukey multiple comparisons of means analyses.

at E-plots but was not statistically different. At L2001, we observed the same tendency as at L2009, and there was a statistical difference between G- and E-plots, though not with control values due to the high variability. At the L1972 site, there was a statistically significant drop

in MR values at G-plots compared with the adjacent intact stand, which was likely connected to the small soil microbial biomass (Fig. 5) and the small number of microorganisms at trophic groups among microsites (Fig. 6). At the control sites, the contribution of microbial

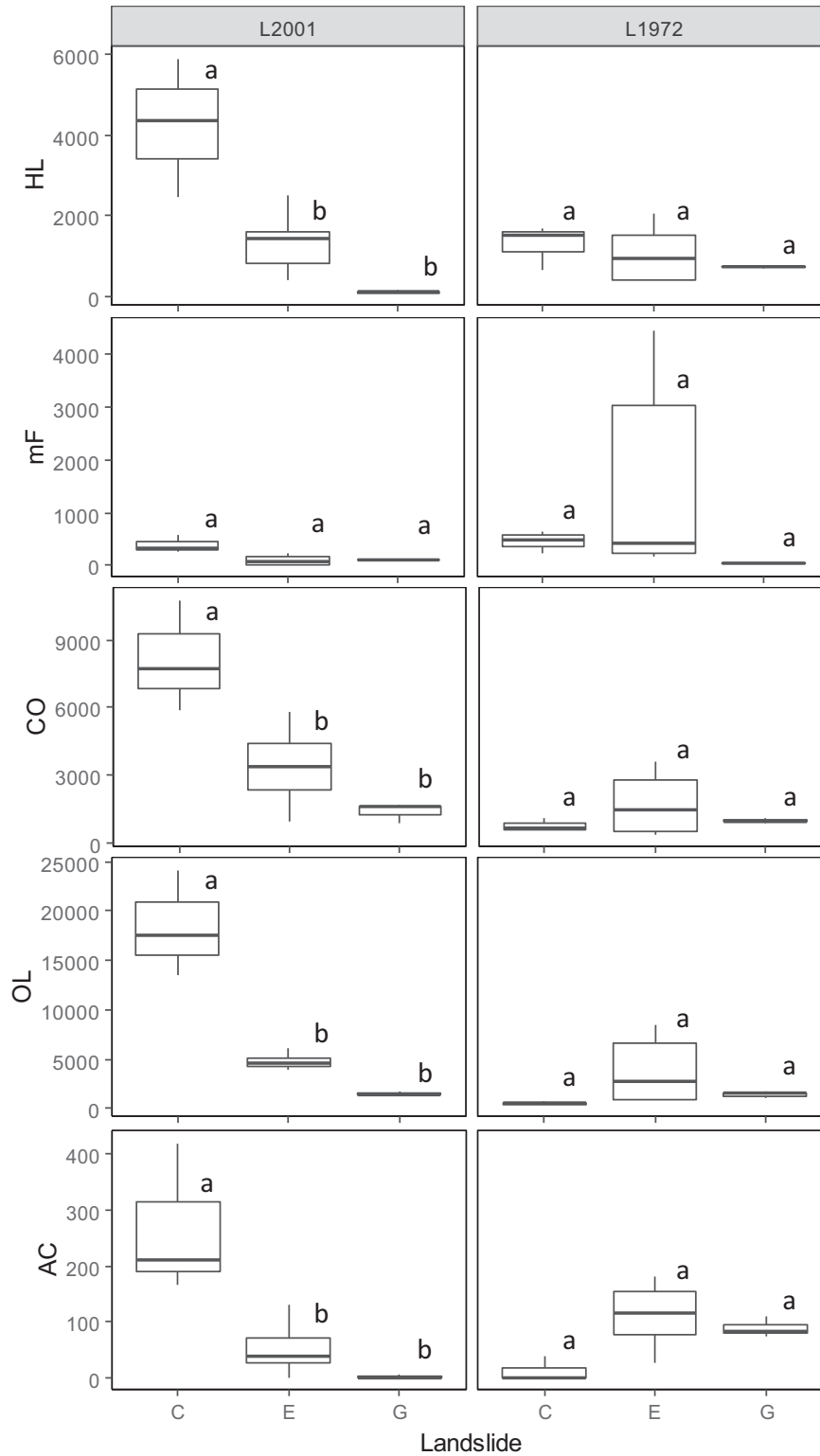


Fig. 6. The effect of a landslide and its microsite type (C – control plot; E – right and left edge of landslide; G – ground; C – control) on number (thousands of CFU g⁻¹ of dry soil) of colonies of hydrolytic microflora (HL), microscopic fungi (MF), copiotrophs (CO), oligotrophs (OL), and actinomycetes (AC) at 0–5 cm mineral soil horizon at landslides of different ages (L2001, L1972). The values are arranged as boxplots (medians with confidence intervals, min, max). The horizontal line within the box indicates the median, the box boundaries (hinges) indicate the 25th- and 75th percentiles, the whiskers indicate the highest and lowest values, and the dots above or below the whiskers indicate the outliers. The medians followed by different letters in the same curve are significantly different at $P < 0.05$ according to Tukey multiple comparisons of means analyses.

respiration to the total soil CO₂ emission was almost the same, at about 11–15% (Masyagina et al., 2013). At young landslide sites (L2009 and L2001), this value was two times higher than that of respective control sites, especially for E-plots. At the older landslide site (L1972), in contrast, microbial respiration contribution was smaller than that at the control sites (Masyagina et al., 2013). The low contribution of microbial respiration at the older site was due to low soil microbial biomass (Fig. 5). The lowest contribution of microbial respiration was revealed at the G-plots, where a successional recovery of vegetation was observed that resulted in increased root respiration contribution to the total soil respiration.

We also examined soil aerobic heterotrophic bacteria via measurements of soil microbial biomass (MB) based on SIR evaluation. The MB values revealed no difference among control stands or landslide sites in the top 5 cm of the mineral soil layer; however, the MB values varied widely depending on the microenvironment: maximum variation was observed at E-plots and was at a minimum at G-plots (Fig. 5). The great variation of MB values revealed at E-plots resulted from the high variation of ecological conditions and the large amount of dead debris mixed with soil O- and mineral horizons after the landslide disturbance. As previously mentioned, minimal values of MB were registered at G-plots at “young” landslide sites (L2009–L2001). In particular, minimal values were recorded at L2009, where we observed a significant decline in microbial biomass at G-plots (along with a high variation of MB at E-plots), which was likely due to the critical deficit of soil nutrients and organic matter (Fig. 4) caused by nutrient runoff due to erosion processes following the landslide. This finding matches well with the low rates of MR and SR found at G-sites at L2009, whereas at L1972, soil microbial biomass at G-plots was comparable with MB values at E plots, which indicates a gradual regeneration of microbiota in mineral soil.

Quantitative PCR was used to examine the abundance of the 16S rRNA genes of bacteria in the top 5 cm of the mineral soil layer. We found differences in the number of bacterial 16S rRNA gene copies at all three control sites, but these differences were not statistically significant. We revealed statistically significant differences in the abundance of the 16S rRNA genes of bacteria among landslides of various age classes and found a similar pattern at every landslide site (E- and G-plots) and the adjacent control site. The abundance of the 16S rRNA genes of bacteria tended to be higher at E-plots and lower at G-plots, and the abundance values at the control site were in the middle position (Fig. 5). At the “old” landslide site (L1972), the abundance of the 16S rRNA genes of bacteria at G-plots was comparable with that of the control site. In general, patterns of temporal changes to the number of bacterial 16S rRNA gene copies and MB values during ecosystem recovery after a landslide disturbance were similar, which points to the quick occupation of disturbed areas by soil heterotrophic and chemotrophic bacteria, which occurs during microenvironment (e.g. ST) recovery.

The sustainability of the soil system is mostly determined by the sustainability of the soil microbial community (Zvyagintsev, 1992). An important parameter of the eco-physiological status of the microbial population is the coefficient of microbiological activity, qCO_2 . A large deviation of a qCO_2 value from “1” points to a disorder of the normal functioning of soil microbiota due to some stress (Anderson and Domsch, 1990). Our analysis of the coefficient of microbiological activity values revealed an intensive disturbance of microflora functioning at the L2009 and L2001 sites and less disturbance at the L1972 site (Fig. 5). The restoration of the eco-physiological status of soil microflora at sites damaged by landslides is therefore very slow. In addition, a disturbance of the eco-physiological state of soil microbial communities at intact stands was observed. The studied territories represent a case of soil microbial coenosis that develops in cryogenic soil, which itself can influence the eco-physiological state of soil microbiota.

4.4. Landslide influence on biotope composition (soil microbiota, plants)

Landslide disturbance essentially changes the environment and is expected to influence the structure of the soil microbial community.

Oligotrophs prevail as a soil microbiota group in permafrost soil microbiota structure (Fig. 6). Oligotrophic bacteria are able to utilize nutrients and small amounts of nitrogen in the soil and are thus essential to ecosystem functioning as this group prevents nitrogen loss in soil and accomplishes a full mineralization cycle of organic matter (Sorokin et al., 2005). Oligotrophs therefore prevail both among other trophic groups at control sites (350–24000 thousand CFU g⁻¹ of dry soil, Fig. 6) and at sites disturbed by landslides (900–8500 thousand CFU g⁻¹ of dry soil, Fig. 6). Soil microbiota at landslide sites were represented mostly by copiotrophs (350–6000 thousand CFU g⁻¹ of dry soil) and oligotrophs due to a low content of insoluble aromatic compounds (e.g. starch, cellulose, or lignin) in soil and many monomeric compounds and amino acids, whereas at control sites, hydrolytic microbiota (700–6000 thousand CFU g⁻¹ of dry soil) were dominant.

Microbiota-occupied permafrost soil and the freezing soil substrate were mostly dominated by so-called psychrophilic or psychrotrophic microorganisms, whose optimum temperature is 15 °C, maximum temperature is 20 °C, and minimum temperature is 0 °C and colder (Zvyagintsev et al., 1999). Among psychroactive soil microorganisms with low-temperature adaptations, there are different taxonomic groups: bacteria (oligotrophs, hydrolytic bacteria, copiotrophs, actinomycetes) and microscopic fungi (micromycetes). Bacteria prevail in permafrost soils due to these soils' low temperature, their periodic overwetting or overdrying of permafrost soil, and a subacid reaction of the soil solution compared with fungi, which are quite sparse in these conditions (Marfenina, 1994).

The contribution of microscopic fungi and actinomycetes changes depending on the succession stage. Thus, at “young” (L2001) landslide sites, the number of fungi (0–234 thousand CFU g⁻¹ of dry soil) and actinomycetes (0–130 thousand CFU g⁻¹ of dry soil) was lower than that of the control site (fungi: 250–600 thousand CFU g⁻¹ of dry soil; actinomycetes: 170–420 thousand CFU g⁻¹ of dry soil; Fig. 6), whereas at “older” (L1972) landslide sites, there was another pattern: the number of fungi (40–4500 thousand CFU g⁻¹ of dry soil) and actinomycetes (30–180 thousand CFU g⁻¹ of dry soil) tended to be higher than that at control sites (fungi: 230–650 thousand CFU g⁻¹ of dry soil; actinomycetes: 0–38 thousand CFU g⁻¹ of dry soil; Fig. 6), which likely points to the recovery of a microbiota community after the landslide. The number of microscopic fungi – as well as their variation – was similar at the control sites of the two solifluctions. The low contribution of most trophic groups of soil microbiota after a landslide resulted from critical changes that occurred after a disturbance (low C- and N availability, lower MSWC, an absence of vegetation, etc.). After some decades, the soil microbial community is expected to recover together with the ecosystem and tree establishment.

Control stands represent relatively stable quasi-climax forest associations with a well-developed tree layer comprised of *Larix gmelinii* and a small number of *Picea obovata* Ledeb. and *Pinus sibirica* Du Tour in addition to an almost-continuous moss-lichen ground cover (Table 2). Crop density varied from 0.4 to 0.7, and the ages of the stands varied from 90 to 200 years. The mean height of the larch trees ranged from 9 to 13 m, and mean diameter ranges from 10 to 20 cm. The level of diversity was not very high, with the number of species ranging from 14 to 33. The forest understory generally consisted of *Duschekia fruticosa* (Rupr.) Pouzar (15–30%), *Salix* spp., *Lonicera pallasii* Ledeb. (1–3%), *Juniperus sibirica* Burgsd., and *Rosa acicularis* Lindley. The number of vascular plant species was restricted due to competition with moss species and niche limitations. The dominant species of ground vegetation at the control plots of L2001 and L1972 were the dwarf-shrubs *Ledum palustre* L. (10–30%), *Vaccinium vitis-idaea* L. (40–70%), and *Vaccinium uliginosum* L. (3–5%) as well as grass species *Vicia megalotropis* Ledeb., and *Festuca ovina* L. Ground cover generally consists of mosses *Pleurozium schreberi* (Brid.) Mitt. (40–60%), *Hylocomium splendens* (Hedw.) B. S. G. (20–40%), and *Aulacomnium turgidum* (Wahlenb.) Schwaegr. (10–20%) in addition to lichens, such as *Cladonia stellaris* (Opiz) Brodo (up to 20%), *Cladonia rangiferina* (L.) Web. (10–60%),

Cetraria islandica (L.) Ach. (1–5%), *Flavocetraria cucullata* (Bellardi) Kärnefelt & Thell. (1–3%), and *Peltigera aphthosa* (L.) Willd. (1–3%). The dry moss *Rhytidium rugosum* (Hedw.) Kindb. dominated, with 90% of the cover of the intact stand adjacent to the L2009 site.

Landslides contribute significantly to the transformation of stands, species composition, and the process of further reforestation and succession. Moreover, distinct vegetation differences between the landslide site and neighbouring forest could clearly be observed (Geertsema and Pojar, 2007). According to our study, the total number of species at landslide sites of different successional stages varied from 48 to 52, which exceeded the number of species at adjacent control sites. The E-plots were disturbed areas, but many plant species as well as seed bank survived in the soil. Therefore, at E-plots, the usual species of intact forest communities neighbored with invasive species (so-called “explerents”) that had intruded from other distant ecosystems to the space released by the landslide. About 25% of the species at the landslide sites did not occur in intact communities and generally became established during the initial stages of the restoration process. Invasive plant species that appeared at E- and G-plots were more hygrophilous than those from adjacent control sites and included *Calamagrostis langsdorfii* (Link) Trin. and *Equisetum* sp. at L2001 and L1972. At E- and G-plots at L2009, we observed the following invasive species: *Potentilla stipularis* L., *Potentilla inquinans* Turcz., *Rubus sachalinensis* H. Lev., *Viola biflora* L., *Polemonium boreale* Adams, *Poa sergievskajae* Prob., *Silene repens* Patr., and *Viola arenaria* DC. In the first years of restoration, the proportion of invasive species was 37%, and after 33 years, it sank to 11%. Additionally, the orchids *Cypripedium guttatum* Sw. and *Dactylorhiza cruenta* (O.F. Mueller) were abundant on the E-plots and demonstrated a cover of up to 20%.

Vascular plants contribute significantly (33–45 species) to the biodiversity of the landslide biotope. Thus, dominant species of a dwarf shrub-herb layer in intact communities – including *Ledum palustre*, *Vaccinium vitis-idea*, *Carex pediformis* subsp. *reventa* (V. Krecz.) Malysch., *Festuca ovina* L., *Campanula rotundifolia* L., etc. – remained at E-plots and actively developed at G-plots, as well. According to Smith et al. (1986), the first colonizers at landslides in British Columbia were mostly shrubs and ferns, followed by tree species (spruce and alder). Lantz et al. (2009) have revealed that during recovery, microenvironments in thermokarst favour the establishment of shrubs. The diversity of vascular plant- and moss species at E-microsites tends to be higher than that of control stands in all age classes of landslide-damaged larch stands (Fig. 7), excluding the number of moss species in E-plots at L1972. The number of lichen species remained statistically lower compared with control sites 30 years after a landslide. This finding was likely caused by increased competition with vascular plants, which succeeded due to higher growth rates in more favourable soil temperature conditions (Fig. 3) that developed at E-plots after landslide disturbances. In the future, we expect a recovery in the number of lichen species in L1972 due to the accumulation of the vast amount of dead wood ready to decompose, which is a good substrate for lichen species.

G-plots located between the edges of solifluction are characterized by an opened and mineralized substrate in which succession is “primary”, meaning that it takes place in a clear space without any plants or their seeds in a substrate (Mirkin and Naumova, 2012). Therefore, in the absence of biological competition, any species of plant communities of a studied region can intrude, and the number of species at G-plots is usually very high. This space is quickly occupied by saplings of tree species (larch, alder, and willow), sparse herbaceous vegetation (e.g. invasive *Carex media* R. Br. or *Urtica dioica* L.), and some species of ferns and *Equisetum*. The number of vascular plant species located between the edges of solifluction was twice that of the control (Fig. 7) due to the establishment of invasive species. The young solifluction (L2009) was quite different from two others, for we observed a decrease in the number of vascular plant species at G-plots. This case can be explained by the absence of seed sources for successional associations disturbed by a landslide. Two other (L2001 and L1972) landslide areas are located

directly in Nizhnyaya Tunguska River valley, where many species of meadow and petrophyte phytocenosis are located, including grassland mesophytes. However, the landslide area of L2009 is located in the valley of a small tributary to the Kochechum River, which is isolated from the abundant valley of the Kochechum River by natural forest communities and bare cliffs. Therefore, at the E- and G-plots of L2009, the number of plant species (petrophyte species prevail and grassland species are sporadic) is limited compared with the adjacent intact community. Mosses and lichens at G-plots are not as numerous as species as control sites, and the recovery of the moss-lichen layer takes a long time (>3 years), which may be due to a substrate stability for occupation by lichens and mosses. Even though the open surface of the G-plot's substrate is a favourable place for colonization by lichens and mosses at primary stages of succession with no competition from vascular plants, lichens and mosses have difficulty establishing the substrate due to water erosion processes from snow melt and summer rainfall. A lichen's thallome is very small and slow growing, and moss rhizoids are not able to penetrate soil deeply, thereby leaving these plants vulnerable to water erosion.

In this study, we also assessed the impact of landslides on forest regeneration. The intact (control) larch stands had a weak recovery potential of 500–2500 seedlings of larch per hectare, which is a widely known characteristic of intact permafrost larch stands. However, *Larix gmelinii* seedlings abundantly appeared at E- and G-plots in the area disturbed by a landslide. The number of these seedlings at landslide plots exceeded that at control plots by 10–30 times (Fig. 7). In comparison, after wildfires (the main disturbing factor in boreal forests), the natural regeneration of larch on burnt areas of similar age varied from 8000 to 25000 per hectare (Prokushkin et al., 2000), which exceeded the number of seedlings in the intact communities by 5–17 times. The successful natural reforestation on solifluction plots occurred due to the availability of the extensive mineralized substrate and a combination of different microenvironmental conditions for seed germination. Some researchers point to the radical changes in soil pH after the landslide. Thus, Lambert (1972) found higher values of pH in soil disturbed by a landslide compared with the surrounding climax vegetation. Burn and Friele (1989) also found that soils of 43-year-old solifluction in Yukon had higher pH values (7.3–7.4) compared with a value of 6.2 in soils under a mature spruce forest. Moreover, according to Prokushkin et al.'s (2010) study, close-to-neutral soil acidity pH values (6.7–7.1) – which were observed at landslides L2001 and L1972 – are optimal for larch regeneration and functioning. All individuals observed at the sites were of seed origin. In the first years after the disturbance, there was clearly a considerable reserve of larch seeds in the adjacent stands that provided dense sapling formations. The *Larix* species is highly competitive, especially in permafrost areas, and we registered the total prevalence of larch in the tree level at E- and G-plots both 4–6 and 35 years after a landslide event. Alder and willow prevailed in the shrub layer at landslide plots due to interspecific competition. In the future, the intensification of root competition among the tree species will begin, and the natural elimination of trees is expected.

The process of stand formation after a fire in permafrost Siberian regions typically takes 50–80 years (Bugenko, 2002). Smith et al. (1986) have revealed that tree cover recovery after landslides is slower compared with the process in logged areas. According to Leibman (2009), at landslide-affected slopes at Yamal (Russia), bare surfaces slowly revegetate with a full regeneration of shrub-moss cover after several centuries. We assume a time interval similar to Siberian burnt areas for reforestation at solifluction plots. The recovery of damaged communities begins with the recovery of species of intact communities. In the first years after a landslide disturbance, hydrothermal conditions and light availability play a main role in the recovery of forested ecosystems. Depending on these parameters and their heterogeneity in space and time, recolonization occurs, and different types of microenvironments can develop. The tree level – which consists of larch as a dominant species and shrubs and dwarf shrubs as additional species – re-establishes itself

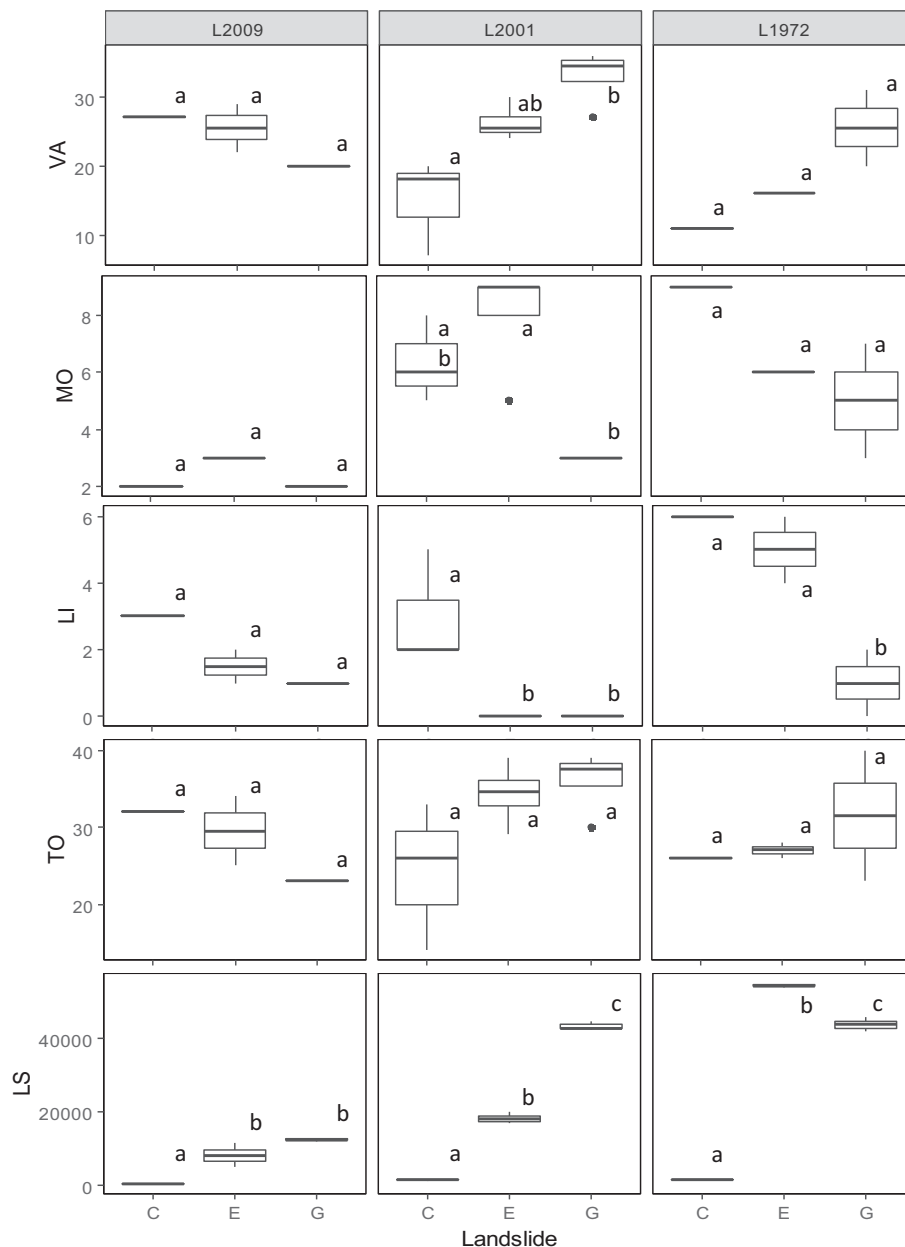


Fig. 7. The effect of a landslide and its microsite type (C – control plot; E – right and left edge of landslide; G – ground; C – control) on the number (pcs) of vascular- (VA), moss- (MO), and lichen (LI) species, the total number of species (TO), and the number of *Larix* seedlings (LS, pcs ha⁻¹) at landslide sites of different ages (L2009, L2001, L1972). The values are arranged as boxplots (medians with confidence intervals, min, max). The horizontal line within the box indicates the median, the box boundaries indicate the 25th- and 75th percentiles, the whiskers indicate the highest and lowest values, and the dots above or below whiskers indicate the outliers. Medians followed by different letters in the same curve are significantly different at $P < 0.05$ according to Tukey multiple comparisons of means analyses.

quite successfully, but moss and lichen cover recovers very slowly. Fallen trees become a substrate for local lichen-moss group formation. The mass accumulation of dead, fallen wood on the margins (E-plots) of the sites later results in the formation of larch-lichen communities, which form in bulging relief at the bottom of washout gullies. Alongside this successional pattern, we could observe the re-establishment of the numerous invasive species. Thus, solifluction processes play an important role in the formation of vegetation cover structure in the cryolithic zone, especially on slopes under intensive insolation. These facts demonstrate the recovery of the initial type of vegetation – a boreal forest with *Larix gmelinii* as a dominant tree species – since larch communities are characterized by a high capability for re-establishment under harsh environmental conditions. However, global climate change continues to influence the future stability and recovery potential of plant communities in the permafrost zone.

5. Conclusions

Landslide processes radically alter the landscape, soil, and biotope. Microecological conditions formed at the initial phase of regenerating succession after a landslide disturbance are far different from those at control sites. Limited soil C- and N availability at all landslide sites compared with that at the control sites confirms that even the “old” L1972 site is far from the state of the control site and that C- and N stocks did not recover after 35 years. The “young” landslide sites of L2009 and L2001 are also spatially very heterogeneous with respect to ecological conditions. The high variation of hydrothermal conditions and microenvironment at the “young” landslide sites resulted in increasing diversity of vascular plants, which led to high soil respiration variation. Similarly, at E-plots of “young” landslides, there was greater soil microbial biomass and microbial respiration as compared with the control. At

the “old” landslide site of L1972, hydrothermal conditions were very close to those of the control sites. At the same time, our analysis of the soil microbial coenosis structure at intact sites as well as at sites disturbed by landslides revealed that oligotrophic microorganisms were ubiquitous. Soil CO₂ emissions at L1972 – which represents the “old” stage of successional recovery – were comparable with the control site and – in some cases – even higher and more spatially variable; however, soil microbial respiration and biomass were lower at both the E- and G-sites. The coefficient qCO₂ points to a stabilization of the microbial community at the L1972 site as it approached the value of “1” and in the area around the control site state (except for G-plots).

Ecological conditions of landslide sites were thus sharply different among the types of microsites as well as at the control sites and were dependent on the age of the landslide. Ecological conditions formed at landslide microsites affected the regeneration processes of newly developing forest in different ways. On the one hand, tree (*Larix* and *Dushekia*) regeneration occurred early during successional period; on the other hand, new pioneer vascular plants not found in the control plots became established at the landslide locations. We found that the total plant biodiversity was 1.5–2 times higher at the landslides than at control site due to the higher number of vascular plants. However, the number of lichen species was significantly lower at the landslide sites than at the control sites. This finding matches well with considerations about landslides as a disturbance process, which increases site biological diversity through changing topography, soil, and runoff conditions (Geertsema and Pojar, 2007).

Our results thus demonstrate that decades after a landslide disturbance, soil changes (such as the decreasing both of C- and N stocks and of microbial activity) in the permafrost conditions of Siberia may persist for decades and have great ecological impact, even if plant diversity and soil CO₂ fluxes remain similar to those at the control site. Similarly, forest ecosystems take decades to recover from landslide disturbance. In addition, the accelerated degradation of permafrost due to landslides hinders the accumulation of soil organic matter.

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Conflict of interest

The authors declare that they have no conflict of interest.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2018.11.468>.

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